

# DIFFERENTIAL INCLUSIONS AS A METHODOLOGY TOOL IN POPULATION BIOLOGY

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## ABSTRACT

Applications of differential inclusions in models of population biology are discussed. It is shown that some problems in population biology like patch selection, optimal foraging, environmental constraints and uncertainty in dynamics and the environment lead naturally to differential equations with discontinuous righthand sides or to differential inclusions. Thus differential inclusions seem to be an unifying framework for models of population biology.

## INTRODUCTION

Investigation of differential equations describing population biology originated from models in physics. Since population biology belongs to “soft sciences” rather than to “hard sciences” like physics, there may be some difficulties to apply the same methodology, i.e. differential equations. In fact, if we construct a model of interacting populations we are faced with the following obstacles that may not conform with the standard theory of differential equations:

1. individuals may exhibit some preferences or strategies (e.g. preference for food, avoidance of predators etc.)
2. there may be some additional constraints that the system should satisfy (e.g. space constraints, nutrient or toxin induced constraints) which are not included into the dynamics
3. there is “uncertainty” in the dynamics (e.g. environmental or demographic noise).

In this paper we show that all the above mentioned problems lead to differential equations with set-valued righthand sides, i.e. to *differential inclusions*. Thus the theory of differential inclusions seems to be promising as a new methodology for models in population biology and, more generally, for models in soft sciences.

Differential inclusions generalize the concept of differential equations. Namely, instead of considering an ODE

$$x'(t) = f(t, x(t))$$

we consider a differential inclusion

$$x'(t) \in F(t, x(t))$$

where the map  $F$  is a set-valued map, i.e. it associates with a point  $(t, x) \in \mathbf{R} \times \mathbf{R}^n$  a set  $F(t, x) \subset \mathbf{R}^n$ . Thus the dynamics is not uniquely given, since there may be more directions in which the system may move. If  $F(t, x) = \{f(t, x)\}$  then we have an ordinary differential equation. Differential inclusions have been thoroughly studied and a fairly complete theory is now available, (Aubin and Cellina 1984; Aubin 1992; Deimling 1992). In these books also differential inclusions with constraints are considered, namely

$$\begin{aligned} x'(t) &\in F(t, x(t)) \\ x(t) &\in K, \end{aligned}$$

where  $K$  is a given closed set which is called the *viability set*. The problem of finding a solution of the above problem is also referred as the *viability problem*. Differential inclusions were also studied from numerical point of view and several algorithms for simulations of differential inclusions are currently available, (Lempio and Dontchev 1992).

## PATCH SELECTION

In (Colombo and Křivan 1993; Křivan 1995) a general framework for including various strategies of individuals to population dynamics was given. This framework depends heavily on the theory of differential inclusions. Here we give one simple example which describes the distribution of a population of predators among two different habitat patches. This is a typical example from behavioral ecology. The density of the population of predators at time  $t$  is denoted by  $x_3(t)$ . We assume that predators move quickly between the two different habitat patches where the density of food is  $x_1(t)$  and  $x_2(t)$ , respectively. Thus at each time instant a part of the population of predators will occupy patch 1 and the rest will occupy patch 2. Let  $u_i(t)$ , ( $i = 1, 2$ ) denote the fraction of the population of predators which are in patch  $i$ . Thus

$$u_1 + u_2 = 1.$$

To proceed further we define the population dynamics in the term of a control system where controls are  $u_1$  and  $u_2$ . Here we choose the simplest Lotka-Volterra like dynamics (Colombo and Křivan 1993)

$$\begin{aligned} x_1' &= a_1x_1 - k_1u_1x_1x_3 \\ x_2' &= a_2x_2 - k_2u_2x_2x_3 \\ x_3' &= k_3u_1x_1x_3 + k_4u_2x_2x_3 - mx_3. \end{aligned} \tag{1}$$

All parameters in (1) are assumed to be non-negative. Solution of (1) is a couple  $(x(t), u(t))$ , where  $x(t) = (x_1(t), x_2(t), x_3(t))$  is an absolutely continuous function and  $u(t) = (u_1(t), u_2(t))$  is a measurable function, such that (1) is satisfied for almost all  $t$ , (Aubin and Cellina 1984; Aubin 1992). In behavioral ecology it is often assumed that each individual behaves optimally in the sense that it maximizes its growth and thus reproduction (Stephens and Krebs 1986). This leads naturally to the maximization of

$$\frac{x_3'}{x_3} = k_3u_1x_1 + k_4u_2x_2 - m \mapsto \text{Max}$$

thus to the following strategy map  $S(x)$  :

$$S(x) = \begin{cases} (1, 0) & \text{if } k_3x_1 > k_4x_2 \\ (0, 1) & \text{if } k_3x_1 < k_4x_2 \\ \{(u_1, u_2) | u_1 + u_2 = 1, u_i \geq 0\} & \text{if } k_3x_1 = k_4x_2. \end{cases}$$

Thus together with equation (1) we have the following optimality constraint on possible controls  $u = (u_1, u_2)$ :

$$u(t) \in S(x(t)). \tag{2}$$

We see that the dynamics (1) is not uniquely given at points where  $k_3x_1 = k_4x_2$ . Thus (1) together with (2) is a differential inclusion rather than a differential equation. We have to show that (i) the model has a solution, (ii) solutions are uniquely defined. Namely the second part, i.e. the uniqueness of solutions may look suspicious at the first sight, since the dynamics itself is not uniquely defined. Nevertheless, using standard results from the theory of differential inclusions and differential equations with discontinuous righthand sides it may be proved that solutions of our model do exist and they are uniquely defined (Colombo and Křivan 1993; Křivan 1995; Kastner-Maresch and Křivan 1995). Moreover, it may be proved that standard numerical methods like Euler method or Runge-Kutta methods or more advanced methods for differential algebraic equations are convergent (Kastner-Maresch and Křivan 1995). In Fig. 1 a simulation of (1) together with (2) is given.

## CONSTRAINTS

Besides the dynamics given either by a differential equation or, more generally, by a differential inclusion

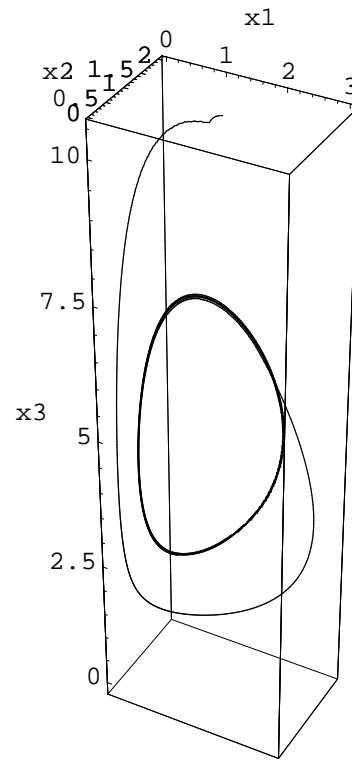


Figure 1: Solution of (5), (7) with  $a_1 = 3.5$ ,  $a_2 = m = k_1 = k_2 = k_3 = k_4 = 1$ .

we may have some additional constraints given by a viability set  $K$ . It is assumed that the system cannot exist outside its viability set  $K$ . Given a dynamics and constraints we may decide whether the system is viable, i.e. whether viable solutions do exist. However, when constructing a model we are often faced with a different problem: How to construct the dynamics such that the constraints are automatically satisfied. Here we show one possible approach for solving this problem (Křivan 1991; Kastner-Maresch and Křivan 1995; Antonelli et al. 1993; Antonelli and Bradbury 1995). We consider two populations denoted by  $x_1, x_2$  which compete for a “space”. The total available space is normalized to unity. Let us assume that those two populations are not limited by anything else than the total space available. We choose the simplest possible dynamics, namely exponential growth for both populations

$$\begin{aligned} x_1'(t) &= a_1x_1(t) \\ x_2'(t) &= a_2x_2(t). \end{aligned}$$

Together with this dynamics we have the constraint

$$x_1(t) + x_2(t) \leq 1$$

which defines the viability set

$$K = \{(x_1, x_2) \mid x_1 + x_2 \leq 1\}.$$

The above system together with the constraint does not have a viable solution. Indeed, starting at a point lying on the constraint line the system leaves immediately its viability set  $K$ . Since this is not possible (from biological point of view) we conclude that the dynamics must necessarily change along the constraint line, i.e. on the boundary of the viability set where the system is not viable. We may assume that on the boundary of the viability set the mortality increases due to the pressure of the environment, e.g. lack of the space. Thus along the constraint the model becomes

$$\begin{aligned} x_1'(t) &= a_1 x_1(t) - m x_1(t) \\ x_2'(t) &= a_2 x_2(t) - m x_2(t) \end{aligned} \quad (3)$$

where  $m$  can be computed by differentiating the condition  $x_1 + x_2 = 1$ . Thus we get

$$m = a_1 x_1 + a_2 x_2 \quad \text{for } x_1 + x_2 = 1.$$

For  $x_1 + x_2 < 1$  we set  $m = 0$ . With such  $m$  the dynamics (3) becomes viable, i.e. all solutions (if any) will satisfy the constraint. However, due to discontinuity of the function  $m$  along the constraint line, (3) becomes a differential equation with discontinuous righthand side. It is well known that discontinuous differential equations may not have a solution. In general, several notions of a generalized solutions for discontinuous differential equations were given. One of them is so called Filippov solution (Filippov 1988). Roughly speaking this is a solution to a certain differential inclusion which arises from the original discontinuous differential equation by convexifying the righthand side at those points where it is discontinuous. Using this approach it may be proved that (3) has a Filippov solution (Křivan 1993). Moreover, it may be proved (via arguments using differential inclusions) that in the above problem solutions of the original discontinuous equation do exist (Křivan 1991; Křivan 1993).

## UNCERTAINTY IN DYNAMICS

In models of population biology we are necessarily faced with the problem of uncertainty. Let us consider a model of population dynamics which is given as an ODE

$$x'(t) = h(t, x(t), u). \quad (4)$$

Here  $u$  denotes the unknown parameter which models the uncertainty or noise. There are two approaches towards this equation. The first one considers  $u$  as a stochastic process and leads to *stochastic differential equations*. However, the statistical prerequisites behind this approach may be difficult if not impossible to verify. Moreover the interpretation of the resulting stochastic differential equation is not straightforward due to various possible stochastic integrals (e.g. Stratonovitch and Itô integral).

The second approach that we want to discuss here is the so called *unknown-but-bounded noise*. This means that the only assumption on  $u$  in (4) is that it belongs to a prescribed bounded set  $U$ , which may depend on time or even on the state of the system. Then (4) becomes a differential inclusion

$$\begin{aligned} x' &\in F(t, x) := \{h(t, x, u) \mid u \in U\} \\ x(0) &= x_0. \end{aligned} \quad (5)$$

The collection of all possible solutions of (4) for different measurable functions  $u(t) \in U$  forms the solution set  $S$  of (5). However, comparing (5) with its stochastic counterpart we see that no probabilistic information is provided together with (5). This is due to the fact that admissible velocities are not distinguished one from another, e.g. all of them are equally likely. An analysis of (5) thus requires the study of infinitely many solutions. If some additional knowledge on the noise is available, e.g. some values of  $u$  are more likely than others, we are faced with the problem of transferring this information on the solution set of (5), in order to give more precise estimates. This may be done via the theory of metric likelihood for solutions of (5), (Colombo and Křivan 1992). It is based on the following idea. The set  $U$  is considered as a *fuzzy set* given through its *membership function*  $\rho : U \mapsto [0, 1]$ . This membership function has the meaning of “measuring how much a point  $u$  belongs to the set  $U$ ”. The less likely points of  $U$  are those with smaller value of  $\rho$ . The value 0 means that a point does not belong to  $U$ , so such an event cannot occur. This membership function allows to consider the set of trajectories of (4) as a fuzzy set with the following membership function

$$L(T, x) := \frac{1}{T} \int_0^T \rho(u(t)) dt.$$

Here  $x$  stands for the trajectory of (5) which corresponds to the control function  $u$ . We note that  $L(T, x)$  denotes the membership function of a solution  $x(\cdot)$  on the interval  $[0, T]$ . Using this membership function we can distinguish those trajectories which are likely to occur, namely we may compute the trajectory with maximal likelihood from those which are not likely to occur. In (Křivan and Colombo 1994), using the median instead of the mean, an analogue of the *mean extinction time*, called *median extinction time* was defined. Applications to exponential and logistic growth were given in (Křivan and Colombo 1994).

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